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THE BIO-MECHANICS OF THE BIRD SKULL

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THE BIO-MECHANICS OF THE BIRD SKULL

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ONCE natural selection began to mold a bird out of ancestral reptilian stock, a point of no return was quickly attained, just as Davis (1960) has described for mammals. The specialization of the forelimb into a wing at the beginning of avian evolution was irrevocable. Henceforth, this member could never again be used, as in ancestral reptiles, to capture food or manipulate objects. Now the bill—toothless and light in weight—took over these functions and more. The upper bill came to be a separate part—movably-hinged to the cranium to form a kinetic skull. In fact the unparalleled versatility of the bill as a tool stems from the achievement of this mobility or kinetism. It was a major adaptation as important to the whole of the class *Aves* as the origin of flight.

PURPOSE OF THIS PAPER

In terms of classical mechanics, the kinetic bird skull is a simple machine, made up of first and second class levers. When it functions, the tip of the upper bill is raised or lowered and the lower bill brought into co-ordinated action by the lever system. This fact, unknown or ignored by the comparative anatomists of the nineteenth century, led to grave errors in higher classification, which should be corrected.

A thorough appreciation of kinetism is essential for understanding future papers on bird phylogeny to appear in this series. The subject was covered briefly in previous papers (Beecher, 1950, 1951, 1953), in which the earlier papers by Moller (1931) and Engels (1940) were also listed. But no attempt was made there to quantify the lever mechanics or to pursue the matter outside the song bird groups then under consideration. This paper attempts to estimate the degree of perfection of the adaptation in related species with different feeding habits; measurements will be applied, calculating mechanical advantage in each case. A number of extreme variations within the general theme of the major adaptation will then be studied to determine whether all fall within the general concept.

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MATERIALS AND METHODS

Jaw musculature was dissected and bird skulls studied for many hundreds of species of birds. The method of recording the extent of skull kinesis was simple but probably adequate for the present purpose. A plastic clamp with claws for the eye orbits and foramen magnum held the skull firmly over a sheet of drawing paper lying parallel to the sagittal plane. The bill tip was then manipulated by hand and tip movement read by means of aligning sights. The degrees of arc traversed by the tip both upward and downward from the position of rest (Fig. 1) were obtained by forcing the bill almost

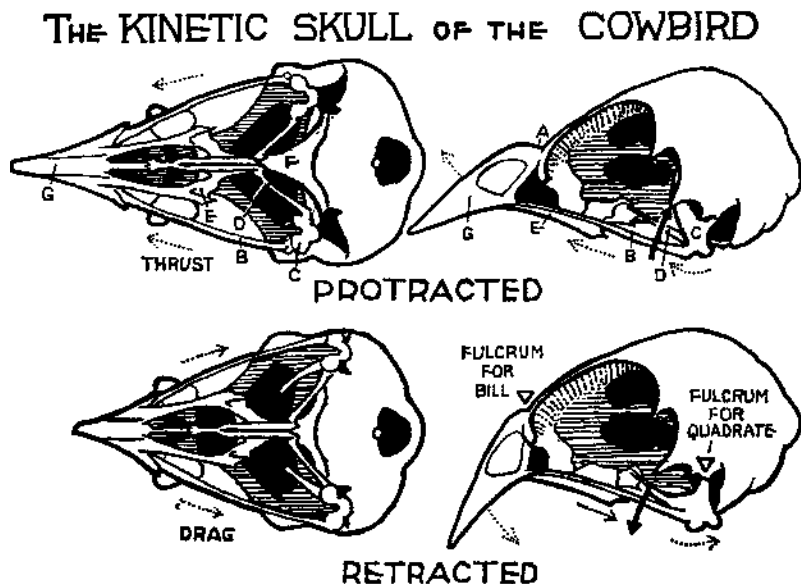


Figure 1. Relationships of the upper bill and palate framework to the cranium of *Molothrus ater* in protraction and retraction. A, naso-frontal hinge; B, jugal; C, quadrate; D, pterygoid; E, palatine; F, sphenoidal rostrum; G, premaxilla plus maxilla.

to the breaking point. This subjective reading is consistently larger than would be obtained indirectly by manipulating the quadrates, but differences among the species studied were of sufficiently large order that the method is believed quite valid. Measurement of the lever arms of quadrate and bill could be made directly and accurately with a caliper rule. From eight to ten skulls of each of the three species illustrated in Fig. 4 were measured ; the figures given are the average ones.

A word about the orientation of the skull illustrations on the page is needed. All birds—in fact, all vertebrates (Beecher, 1951b ; Duijm, 1951) —have a characteristic orientation of the head in space when at rest. It is the attitude in which the inner ear assumes its position of strain-less balance in the gravitational field, with the macula of the utricle and the external semicircular canal in the horizontal plane. It is a matter of utmost significance that the skulls of birds have *rotated* around the inner ear to achieve a bill orientation and eye orientation most advantageous to the feeding adaptation of the particular species. Thus, the bills of finches and blackbirds (Icteridae) are characteristically oriented a little above the horizontal, as in ostriches. The bills of shore-birds are oriented downward, that of the woodcock so fantastically that the bones of the palate are crowded forward onto the floor of the upper bill. Such relationships have had far-reaching effects on the jaw musculature. Their discussion is left to a future paper long in preparation, but it is desirable—in view of future work—to correctly orient the skull on the page.

HOW THE MACHINE OPERATES

When a bird skull that has been cleaned and dried is placed in boiling water for about 30 seconds, the upper bill may be moved up and down on its articulation with the cranium—a hinge formed of the thinly-interlaminated nasal and frontal bones. However, in the living machine these movements are initiated in the quadrate which is movably-articulated both to the base of the cranium and, via the bony palate framework, to the base of the bill. In keeping with its strategic position, the quadrate is intriguingly designed, with bony processes for projecting forces in precise directions. The largest is the orbital process—an unmistakable lever. The muscle which in-

serts on its tip and originates on the medial surface of the jaw (Fig. 2, *M. pseudotemporalis profundus*) sets in motion a remarkable chain of events. Its contraction draws the lever powerfully downward, rocking the quadrate backward on its cranial articulation (Fig. 2, 5), acting in the role of a fulcrum.

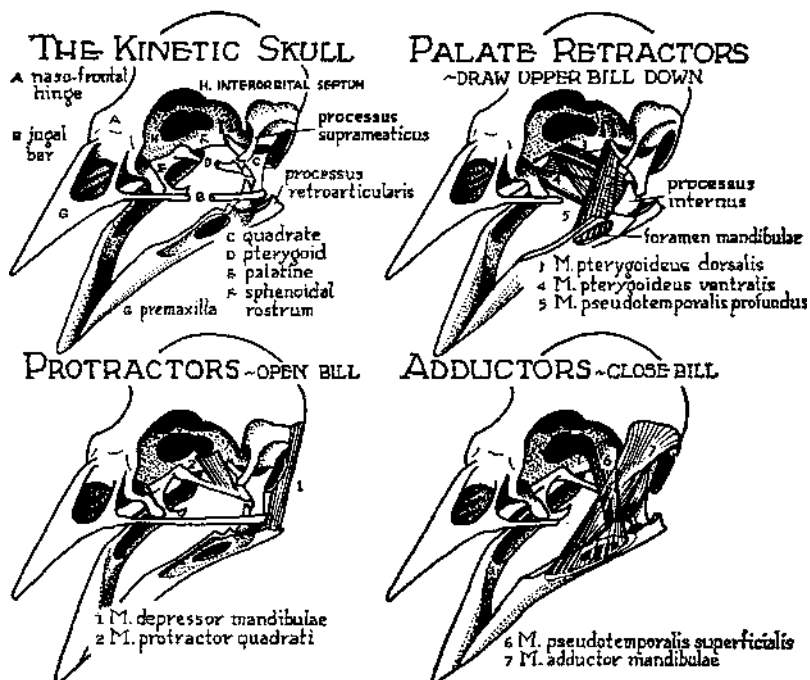


Figure 2. Mass functions of muscles (Redrawn from Beecher, 1951a).

The drag thus exerted on the jugal arch (B) draws the bill tip downward on its naso-frontal hinge, here in the role of fulcrum for the bill lever. As Mattingly (1953) has pointed out, the quadrate in this action is a bent first class lever, the bill a second class lever (Fig. 3). The quadrate at the same time also moves a rod-like bone articulated to its short medial process—the pterygoid. Since the pterygoid is articulated to the palatine, which is fused to the maxilla (Figs. 1,2), a triangular frame of bony rods links the quadrate on each side of the skull with the lateral and medial base of the upper bill. The paired triangles of the palatal frame fuse at midline

into a palato-pterygoid clasp, sliding on the guide rail of the sphenoidal rostrum with the smoothness of a precision machine.

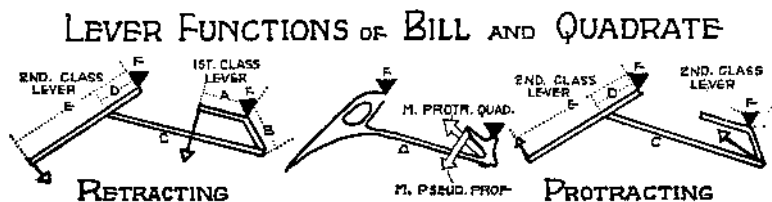


Figure 3. Diagrammatic analysis of lever mechanics (based on Mattingly, 1953). A, effort arm of quadrate; B, resistance arm of quadrate; C, jugal; D, effort arm of bill; E, resistance arm of bill; F, fulcrum.

The reverse action of this system elevates the bill tip. It is initiated by an opposing muscle (Fig. 2, *M. protractor quadrati*), which originates on the medial wall of the interorbital septum and inserts on the body of the quadrate—and on the head of the pterygoid where it articulates with the quadrate. The contraction of this muscle rocks the quadrate forward on its cranial fulcrum, and now the quadrate acts as a second class lever. The forward thrust of the jugals and the pterygoid-palatine linkage, delivered to the base of the bill, elevates it on its naso-frontal hinge. This hinge again acts as the fulcrum of a second-class lever—the bill. Here it should be noted that the jugal and palatine bones are thin where they articulate with the bones at the base of the bill—mainly maxilla—to form further hinges of bones that bend. Possibly this type of hinge is not found outside of birds but some birds have a real ligamentous hinge for the jugal connection to the bill—the parrots, for instance, and the parrot-billed cardueline finches *Mycerobas* and *Eophona*.

Neither of the antagonistic muscles moving the quadrate functions alone. The action of *M. pseudotemporalis profundus* (Fig. 2, 5) in drawing the tip of the bill downward is aided by two slips of *M. adductor mandibulae* (7), originating on the quadrate body, and by the palate retractors, *M. pterygoidens dorsalis* (3) and *ventralis* (4). The action of *M. protractor quadrati* (2) in elevating the tip of the upper bill is aided by the contraction of *M. depressor mandibulae* (1) in depressing the mandible or lower bill. The mandibular head of the quadrate thus becomes the fulcrum for another first

class lever—the third and final lever in the kinetic avian skull. Finally, the adductor mass, made up of *M. pseudotemporalis superficialis* (6) and *M. adductor mandibulae* (7), not only raises the lower bill but, due to the posterior pressure of its articulation with the mandibular head of the quadrate, helps to rock the quadrate backward on its cranial articulation. Thus it aids the action of *M. pseudotemporalis profundus* in drawing the upper bill down against the lower. So, there is a highly co-ordinated interplay of muscles for any action of this lever machine.

The lever relations are shown diagrammatically in Figure 3, which expresses the fact that the bill is always a second class lever but that the quadrate is a second class lever only under the action of *M. protractor quadrati*. Under the action of *M. pseudotemporalis profundus*, the quadrate is a first class lever.

RESULTS OF THE STUDY

Shorter-billed Species.—Let us first examine the engineering to be seen in the skull itself, ignoring the musculature. This could hardly be shown better than in a series of related genera taken from the American blackbird family, Icteridae, and Fig. 4 is modified from my study (1951, Fig. 2) of that

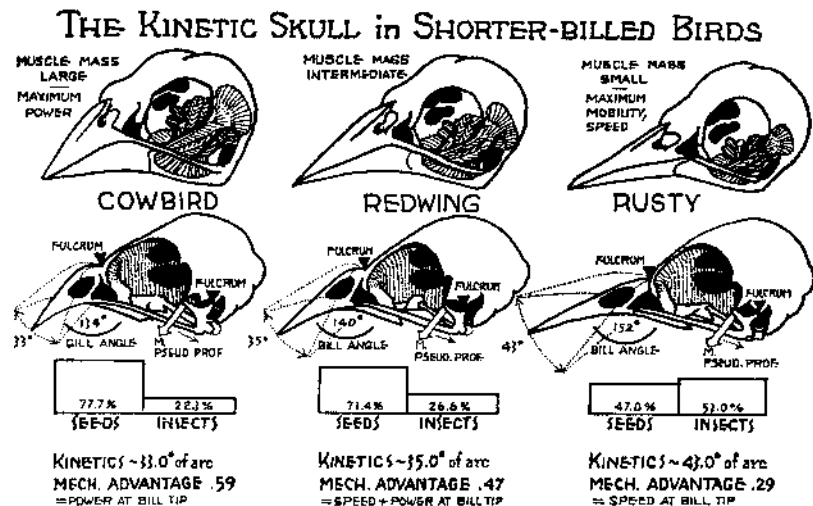


Figure 4. Mechanical advantage in the bills of related species with differing diet

family. The choice of species—the cowbird (*Molothrus*), redwing (*Agelaius*) and rusty blackbird (*Euphagus*)—was based on exceptionally good information about their relationships and diets. In comparing the skulls for mechanical advantage, a formula used by Mattingly (1953) was employed. The for-

mula is expressed as $MA = \frac{A}{B} \times \frac{D}{E}$, where A is the effort arm of the quadrate and B, the resistance arm, and where D is the effort arm of the bill and E, the resistance arm (Fig. 3).

When this formula is applied to these genera, the highest figure for mechanical advantage occurs in the cowbird (.59) and the lowest in the rusty blackbird (.29), the redwing (.47) falling in between. This means that the cowbird bill has the greatest mechanical power at the tip and the rusty blackbird the least. But, since speed is the inverse of power, we may say that the cowbird has the least speed at the tip and the rusty blackbird bill, the most.

These facts are in good agreement with the kinetics studies, which showed that the cowbird bill has the lowest mobility (33° of arc) and the rusty blackbird, the most (43°), with the redwing (35°) again intermediate. It also fits the known diets of the three, expressed in block diagrams in Figure 4. Cowbird seed-cracking for instance requires a relatively small gape with a minimum of upper bill movement and maximum power. The longer-billed rusty blackbird has greater bill movement, associated with more insectivorous diet. It has a larger gape and needs the maximum of closing speed at the tip of the bill. In typical insect-eaters, like flycatchers, we actually hear the closing snap of the bill.

A still further mechanical advantage is seen in the angulated commissure of the seed-adapted cowbird. This is the downward angle of the tomium or cutting edge of the upper bill relative to the jugal, measured in the rest position. This angle is 134° in the cowbird, 140° in the redwing and 152° in the rusty blackbird. The highly angulated commissure as seen in the cowbird is a typical finch adaptation. It enables the cowbird to bring the large mass of the pterygoideus muscles (Fig. 2 - 3,4) into the most effective use, viz. at nearly right angles to the cutting edge of the bill. Thus the powerful retraction of the palate and depression of the upper bill is

equal to the powerful elevation of the mandible or lower bill by the adductor mass (6,7) . The progressively lesser degree of angulation in the redwing and rusty blackbird decreases the retractive power of the pterygoideus mass on the bill tip, substituting speed instead.

Finally, in our examples, there is a difference in the total muscle mass itself. Gross inspection reveals thicker, more extensive jaw musculature in the cowbird, which is greatly reduced in the rusty blackbird—the redwing again falling in between. But even the structure of the cowbird muscle makes for greater power and that of the rusty blackbird for greater speed. All three genera have pinnate adductors muscles in which the individual fibers do not run from origin to insertion as in parallel muscles. Pinnate muscles have short fibers, running herring-bone fashion to meet on raphe, and such muscles retract with greater power but less shortening (Grant, 1942) . But the fibers are shorter in the cowbird and meet the raphe at a more obtuse angle and they are longer in the rusty blackbird, meeting the raphe at an acute angle more nearly approaching the parallel condition. Hence the musculature agrees fully with the bony architecture. The cowbird musculature will contract with greater power ; the rusty blackbird musculature will contract with greater speed ; the redwing musculature will lie in between.

It is worthwhile to pursue other series of related genera and species whose adaptations range from seed-eating to insect-eating. The African weavers of the family Ploceidae furnish examples similar to those drawn from the Icteridae, all within a single genus, *Ploceus*. In the series illustrated in Figure 5, *Ploceus cucullatus* (22°) leans heavily to seed-eating while *P. aurantius* (30°) is primarily an insect-eater. The diet

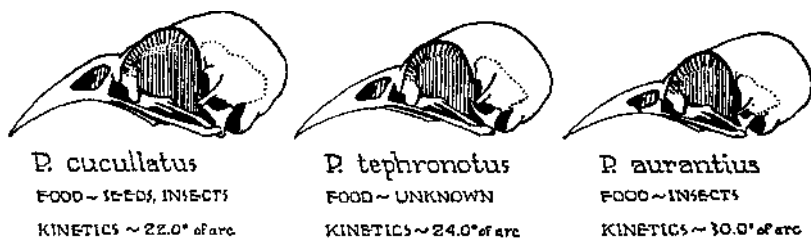


Figure 5. Reduction of mechanical advantage for insect diet within the genus *Ploceus*

of *P. tephronotus* (24°) could not be determined but is presumed to be intermediate. In this series, as in the icterid series, the seed-cracking *cucullatus* has a more angulated commissure and a longer orbital process of the quadrate, as well as decreased kinetics. The bill would have greater closing power at the tip. In *aurantius*, with its insectivorous diet, we find decreased angulation, a shorter orbital process and increased kinetics. The bill would have greater speed at the tip, less power. In all of this *tephronotus* would be intermediate.



Figure 6. Reduction of mechanical advantage with shortening of orbital process of quadrate in the tanagers, *Buthraupis* (left) and *Compsocoma* (right).

But even in tanagers (family Thraupidae), which do not have the commissure so highly-angulated, the long orbital process seems to be correlated with power and with reduced kinetics.

Buthraupis, with its long orbital process (Fig. 6), has the skull less kinetic (27°) than *Compsocoma*, with a shorter orbital process (31°). In another tanager series, the orbital process is longest in *Piranga roseogularis* (27°), shorter in *P. olivaceus* (36°), and shortest in *Ramphocelus* (50°).

A particularly good example of the whole series of changes that take place when a seed-eating stock secondarily evolves species adapting to insectivorous diet is seen in *Melospiza* (Fig. 7). The song sparrow, *M. melodia* (adult), is primarily a seed-eater with low kinetics (21°). With greater insect diet, Lincoln's sparrow, *M. lincolni*, shows increased kinetics (27°). With still greater insect consumption, the swamp sparrow, (*M. georgiana*) increases kinetics still more (31°), and reduces muscle mass notably. In each case, comparison with the dotted line in Fig. 7 (drawn at an angle of 48° to the base-line), indicates a decrease in the angulation of the commissure with increased insect diet. The orbital process also gets shorter as kinetics increases, increasing speed at the tip.

The case of the juvenal specimen of *M. melodia* is interest-

ing. All young passerine birds have the wing of the ethmoid too short to reach the jugal bar. Since this wing serves as a guide, limiting the upward movement of the bill tip in adults,

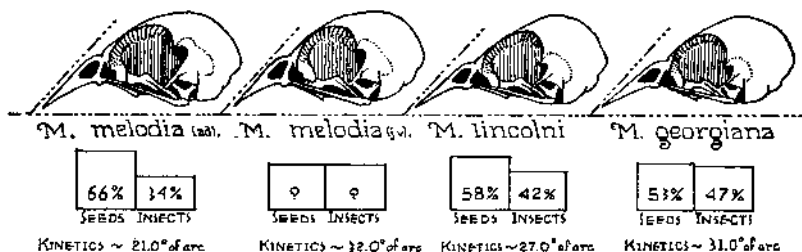


Figure 7. Reduction of mechanical advantage and increase in kinetics with increased insect diet in the finch genus *Melospiza*. Note adaptive increase in kinetics in juvenal *M. melodia* due to undeveloped ethmoid wing.

kinetics is thus increased in juvenal *Melospiza melodia* (32°) and, probably, in all young passerines. I have noted it for young crows and a few other species. The meaning of this seems clear. In the very young nestling bird, the universal adaptation is toward an enormous gape, a target for the needed protein insect food, delivered by the adult. When the young bird leaves the nest, its diet may still be insects for a considerable period, even in the case of the song sparrow which, as an adult, will eat mainly seeds. The deficiency of the ethmoidal wing in the juvenal thus appears adaptive.

But it is quite clear that the musculature is much more complicated than has been described here. Hofer (1950) gives a more detailed treatment of the various muscle slips which may make up, for instance, the adductor mass, and Moller, as early as 1931, called attention to the fact that the angle of attack of a muscle changes as the bony parts are moved. As an example, the pterygoideus musculature, originating on the palatine and inserting on the internal process of the mandible, first elevates the mandible and then retracts the palate, tending to co-ordinate the closing of the bill. The adductors, too, tend to draw the upper bill downward by pressing the mandible against its articulation with the quadrate—but here it is necessary that *M. pseudotemporalis profundus* first draw the orbital process downward. If this does not happen the

bill movements would be out of co-ordination and the pressure caused by the adductors would push the quadrate and palate upward and forward, elevating the upper bill.

However, this does not happen and the real point is that there is perfect co-ordination of the musculature to produce exactly the required pressure of the two parts, whether the bill is empty or closing on an object.

Moller mentioned another function of the bill—that of rasping. This is accomplished by interplay of the pterygoideus and adductor masses. The object held is sawed by the cutting edge of the lower mandible while it is held against the horny palate of the upper bill. This is important in the hulling of seeds by some finches.

A different and remarkable type of rasping occurs in the grackle, *Quiscalus* (Beecher, 1951-2), which cracks a hard kernel of corn or an acorn by scoring it completely around its shorter diameter by means of a sharp, horny projection or "knife" (Fig. 8), which is a feature of the horny palate. Here



Figure 8. Kinetic cutting action of upper bill independent of lower bill in *Quiscalus*.

it is the upper bill which is active. As the acorn is rotated by the tongue, a straight line is impressed all around, preparing it for the powerful adduction that breaks it open. The writer has filmed and analyzed the action. The elevation and depression of the upper bill takes place in a quarter of a second for one complete cycle, but the opening of an acorn may take half a minute or more. The sawing action is continuous but the rotation of the acorn by the tongue indicates rhythmic relaxations of the jaw musculature while new "bites" are made, often accompanied by slight forward thrusts of the head. This sawing action involves the rocking of the quadrates and a back

and forth sliding of the palatal framework by the protractor muscles while the adductors hold the object. This adaptation is more interesting because it is used only in autumn. With the normal fruit and insect food of the grackle on the wane, it can live well in the north on acorns after most other birds have migrated south.

Among short-billed birds the parrots have a unique skull type, serving somewhat the seed-cracking function of grosbeaks among the finches—but the adaptation is accomplished differently and cast on a grander scale (Fig. 9. The black cockatoo, *Calyptorhynchus*, easily cracks ivory nuts with its massive bill—a task which humans may accomplish only with a hammer and anvil!

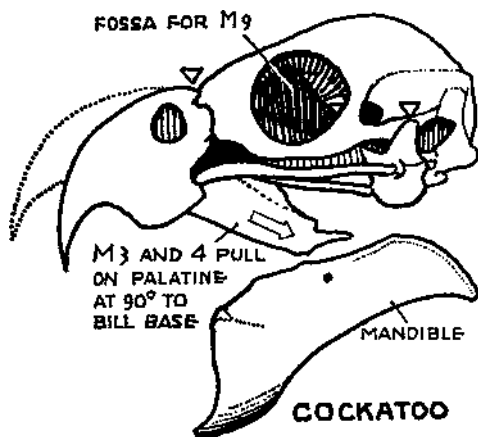


Figure 9. Recasting of the skull in parrots for powerful adduction.

The skulls of parrots represent a rather complete recasting of the avian skull, with some new features. The bill is depressed from 20° to 35° in normal head attitude, and the bill and anterior skull have been telescoped antero-posteriorly without shortening the palatines and pterygoids. Thus the latter have "overlapped" in making their palatine articulation far forward along the sphenoidal rostrum. The wings of the palatines extend posteriorly almost to the quadrate, and this is possible only because they have been tilted to lie almost in the sagittal plane. They also join the maxillae at the base of the upper bill at right angles, so that the power of the palate

retractors—the pterygoideus muscles—greatly aids the adductors in bringing to bear on hard objects. In parrots, too, the lacrymal (fused with the small ectethmoid) elongates—often joining the postorbital process of the squamosal to form a ring of bone around the orbit.

To power this unique skull machine, parrots have evolved two new muscles (adding to the standard seven jaw muscles in birds is almost unique in itself) , and lost one (equally unusual) . One of the new muscles is *M. ethmomandibularis* (9) , which originates high on the anterior part of the interorbital septum to insert on the dorsal process of the mandible (not shown in Fig. 2) . Lakjer (1926) considers it part of *M. pseudotemporalis superficialis* and *profundus* (6 and 5) but I agree with Hofer (1950) that it seems more likely to be part of *M. pterygoideus* (4) , called into play as an adductor. *M. pseudomasseter* (8) is a new muscle also. It originates on the suborbital ring and the jugal bar, inserting on the lateral surface of the mandible, evidently as an offshoot of the adductor mass (7) . Hofer has discussed it thoroughly. *M. pseudotemporalis profundus* (5) is missing (as in cormorants, boobies and whippoorwills) and its lack places the entire responsibility for palate retraction on the pterygoideus.

The orbital process of the quadrate is correspondingly small and appears to be regressed with the loss of its key position in rocking the quadrate backward. *M. protractor quadrati*, on the other hand has very good development with a broad origin on the interorbital septum and insertion over most of the median surface of the quadrate. This is the muscle which lifts the upper bill on the naso-frontal hinge—this time a *real* hinge—and upper bill movement in the parrot is so obvious that it was early discovered, and thought at first to be unique among birds. The use of the upper bill in climbing brings the pterygoideus musculature into action without the contraction of the adductors. The head reaches out, the upper bill protracting ; contact is made and the bill retracts with a kind of tug ; then the cycle repeats.

The important point, for purposes of this paper, is that the parrot skull fits the general adaptation, despite loss of one muscle, almost universally present in birds and the acquisition of two additional muscles—an almost unheard-of occur-

rence in the bird jaw musculature. The special modifications for great bill power evidently called for rather complete rearrangement of musculature.

Contrary to universal belief, the kinetism of the parrot bill is not among the highest. For *Cacatua* (Fig. 9) it seems to be 27° and the mechanical advantage of the skull lever system, about .39. But this figure gives an incorrect impression and cannot be compared with the figure obtained for the cowbird, for example. The angulation of the commissure, discussed for finches, here reaches its greatest expression. The huge muscle mass is mobilized at the most advantageous angle for maximum power at the bill tip.

Long-billed Species. —In the longer-billed bird species changes have occurred adaptively which tend to obscure the fact that they are but extreme cases of the kinetic skull mechanism. This could hardly be said of the skull of the least bittern, *Botaurus lentiginosus* (Fig. 10), which functions very

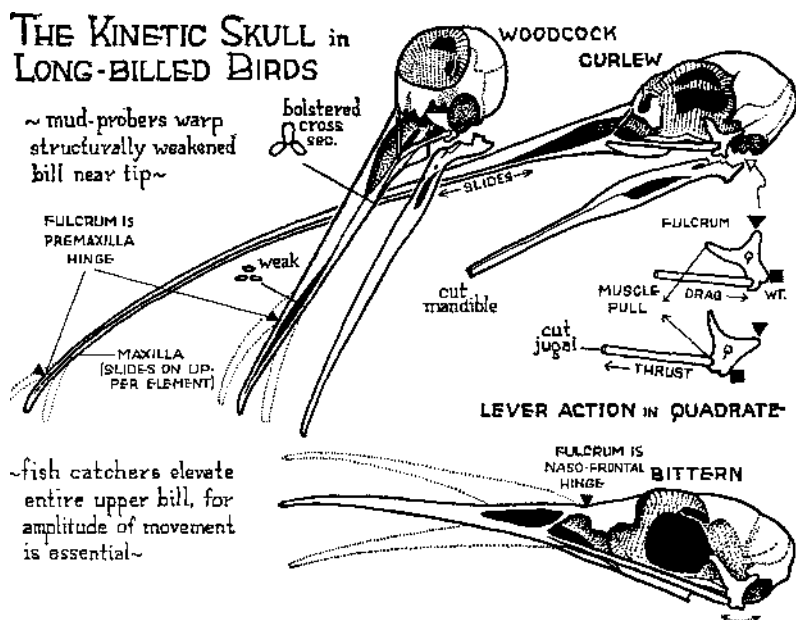


Figure 10. Hinge kinetics and kinetics at a distance in long-billed birds.

much like that of the passerines just considered. There is a naso-frontal hinge, a quadrate with a long orbital process,

and ample kinetics. If we apply Mattingly's formula, we get a figure of .18 which is probably not comparable to the figures obtained for the series of icterid species above because of the distant relationship and very different adaptation. For instance, there is no evidence that the bittern bill tip actually moves with more speed than that of the rusty blackbird with a figure of .29. We would have to consider the fact that the latter has a partly pinnate retractor musculature while that of the bittern is all parallel. The metabolic rates of the birds would also be very different. So the conclusions of an engineer, based only on lever mechanics visible in the skull, would be wrong ; this is a study in biomechanics and a mechanical comparison of distant species cannot at present be given.

But the long bills of the woodcock, *Philobela*, and curlew, *Numenius* (Fig. 10) , are clearly different functionally from those studied above. First of all, there is no naso-frontal hinge. Where it should be, the vertical wall of the inter-nasal septum (missing in the species above) is continuous with the interorbital septum and fused to the nasals and frontals. The skull is quite obviously engineered in these two species *not* to bend at the naso-frontal suture. A cross-section a third of the distance down along the upper bill from the naso-frontal suture shows it to be composed of two lateral elements, the maxillae, surmounted by a single element representing the fused premaxillae. All are highly cancellous for lightness and tubular for maximum rigidity. They are also quite separate and free of each other. A similar cross section made a third farther along the bill would reveal all three elements much diminished in size and strap-like in the horizontal plane. The bill is, in fact, structurally weakened at this point so that the protractor musculature may bend it up at the tip and so that the retractor musculature may bend it down. Thus, all of the quadrate and palatal musculature acts only to produce a sliding motion of the paired maxillae along the single premaxilla. But, since all are fused together at the tip of the bill, this sliding must warp the end third of the bill up and down. Thus, the greatest possible rigidity for mud probing is achieved, coupled with flexibility at the tip in the horizontal plane only. The tactile tip of this upper bill encounters an earthworm and

may lift a bit to grasp it. The lower bill has a long retroarticular process with a large *M. depressor mandibulae*, permitting it also to increase the opening at the tip. It is found that pressure on this process in the freshly-killed bird elevates the end third of the upper bill. Thus, despite the fact that the *M. protractor quadrati* is enormous (its origin occupying the entire interorbital septum) , it seems evident that the *M. depressor mandibulae* — even while lowering the lower bill — is also helpful in elevating the upper bill. Together, they form a powerful protractor musculature, needed to act against the counter-pressure of the earth when the closed bill is thrust deep, then opened at the tip.

In view of the need for rigidity, note that the paired maxillae and the single median premaxilla in the first-mentioned cross-section are not exactly tubular but rather elipsoidal, and oriented for maximum rigidity of the basal portion of the bill. The bill tip is also rigid because of the antagonistic action of opposing muscles. But even when these muscles act to elevate and depress the upper bill-tip, the paired maxillae slide along the premaxilla with no sacrifice of rigidity in the basal three-fifths of the bill.

After these studies were made, the writer discovered that Kripp (1933) had studied geometrical relationships in the skulls of the European woodcock (*Scolopax*) and snipe (*Gallinago*). He compared the differential sliding of the woodcock premaxilla and maxillae, fused at the tip, with the warping of a bi-metal, which, strangely enough, was my own first thought.

Naturally, the effort arm (Fig. 3, D) and resistance arm (E) of the bill cannot be measured at the naso-frontal suture in the woodcock and curlew, as in previous species considered. The measurements must be made where the structural weakening of the premaxilla allows bending to take place. For whatever it is worth the figure for mechanical advantage in the woodcock is .13 and for the curlew, .18. In some ways the bill-tip kinetics of the long-billed curlew, *Numenius americanus* (Fig. 10) , is more remarkable — especially in that movement at the tip is still more remote from the musculature originating it. But it is still the rocking of the quadrates under the action of protractors and retractors

which transmits forces along jugals, palatines and maxillae to bend the fixed premaxilla just at the tip. Again, it demonstrates a kind of engineering found only in birds in which the rigidity of bone is balanced against its flexibility. When thin enough, bone bends like a flat spring and may be used as a hinge.

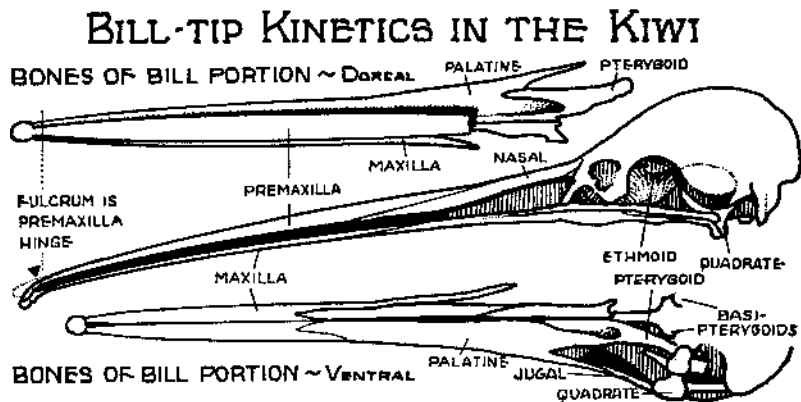


Figure 11. Rigidity for probing in long *Apteryx* bill with extreme tip kinetics.

There remains even a better example of this in the flightless New Zealand kiwi, *Apteryx australis* (Fig. 11), Marshall (1960) expresses the general view when he observes that the kiwi skull is akinetic, because it "requires a rigid beak for use as a probe". There is no doubt that the upper bill is rigid and that the internasal septum prevents any hinge action in the naso-frontal region as effectively as in the woodcock and curlew. The inflation of the ethmoid in adaptation to an unusual sense of smell has placed such a hinge out of the question.

But the skull of the kiwi is, nevertheless, kinetic — *just at the very tip!* Had Marshall seen the musculature in *Apteryx* — a powerful *M. protractor quadrati*, powerful *M. pseudotemporalis profundus* and strong *pterygoideus* (though adaptively simplified as in all ratites) — he would have looked for kinetics. He would have found it in the structural weakening of the premaxilla at the very tip with corresponding weaken-of the maxilla just below it — the two articulating at the bill

tip. Movement is limited, and the corresponding effort for protraction of the lower mandible, when the upper is elevated, would not be as powerful as in the woodcock. There is entirely lacking the lever-like posterior extension of the retroarticular process beyond the point of articulation of mandible with quadrate. Since the upper bill is longer than the lower, its tip must be bent down upon the tip of the latter in capturing prey.

The open sutures of the kiwi skull permit us to determine the relationships of the nasals, premaxilla, maxillae, and palatines quite clearly. In the woodcock the closed sutures of the adult make this impossible. We see also that in the kiwi the palatine and pterygoid are fused. McDowell (1948) interpreted this to be a consequence of the akinetic bill. Since the bill is kinetic his explanation is not valid. Rather, I would say, there is no articulation between pterygoid and palatine in *Apteryx* because there is no need for one. The pterygoid and palatine are virtually in the same plane with each other and with the maxilla. So the force applied by the quadrate may be transmitted to the tip end of the maxilla with great directness down the entire length of the ventral bill portion of the skull (Fig. 2) without bending. The basipterygoid processes serve as stops or guides, since both the upward swing of the orbital processes of the quadrates and the contraction of the paired *M. protractor quadrati* force the pterygoids toward the midline. In the original Archosaurian ancestors of birds, the basipterygoid processes (Simonetta, 1960) were evidently pivots for the metakinetic skulls — in which the snout and cranium had restricted movement via ligamentous articulation with a hinge behind the parietals. Their presence in relatively few birds is generally considered to be primitive and is functionally related to restricted movement. In the woodcock they function as in the kiwi, except that — due to the strong angle between palatines and pterygoids because of the downward orientation of the bill — there is no fusion of palatines and pterygoids.

Basipterygoid processes occur in the other ratites (flightless birds, lacking keels) in correlation with the same restricted kinesis, but the jaw musculature would, again, argue against any extant species being actually akinetic. There is particularly good development of *M. protractor quadrati* and *M.*

pseudotemporalis profundus in all ratites dissected : the ostrich (*Struthio camelus*) , rhea (*Rhea americanus*) , cassowary (*Casuarinus unappendiculatus*) , and kiwi (*Apteryx australis*) . The pterygoideus musculature, while reduced, is still powerful. This suggests at least limited kinetism, possibly aided by open sutures between nasals and pre-maxillaries, as suggested by Simonetta (1960) .

The basiptyergoid processes, though considered primitive reptilian characters, are certainly adaptive in the flightless birds. The broadening of the bill portion of the skull and relative small size of the braincase has necessitated the elongation of the processes so that they may limit the inward movement of the pterygoids upon protraction of the upper bill. The occurrence of the process in the whippoorwill, *Caprimulgus*, where it seems to limit the movement of the thin pterygoid, preventing it from rubbing against the basisphenoid, suggests that it is adaptive for this purpose rather than relict. Its occurrence in the young of Larinae but not the adults again suggests a guiding function of the basiptyergoid process where bones are weak or stress is great.

In the tinamous — not ratites but generally linked with the group by ornithologists — the skull displays a type of kinetism allied to that in the woodcock but seen in a less specialized

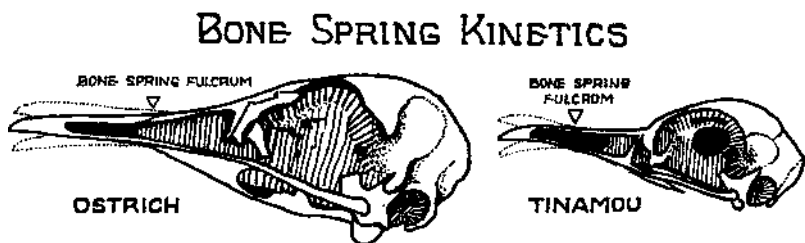


Figure 12. The springing of relatively thin premaxilla and maxillae by the jaw musculature in species lacking the naso-frontal hinge.

version. The skull of *Tinamus major* (Fig. 12) has the premaxilla and the paired maxillae very thin, so that the raising and lowering of the upper bill tip is done by warping the entire mid portion of the bill. In this gradual sort of bending, the premaxilla and maxillae act as flat bone springs. Once more we find birds making use of a device found nowhere else in the tetrapods — the bending of thin bone by antagonistic

muscle systems. It is true that there is a squamous suture with the nasals in the case of the premaxilla in the spring area and a similar suture of the maxillae with the palatines below. But these are closed sutures and there is no question that the bone bends over a broad area, not sharply. It may be that the same thing occurs slightly in the ostrich (Fig. 12) and rhea skulls, but the bone may be too thick to perform this sort of function. This will have to be tested in live or freshly-killed specimens. Boiling massive museum specimens, long dry, may not approximate the flexibility of living bone.

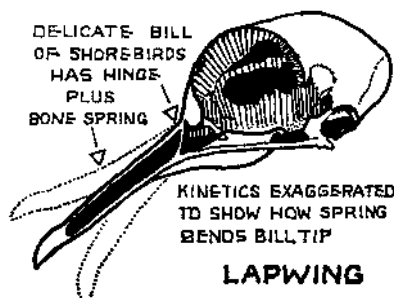


Figure 13. Combination of spring and hinge kinetics in shorebirds.

The bending of premaxilla and maxillae in the slender, delicate bills of shore-birds — the plovers and sandpipers — is even more impressive (Fig. 13). But here it is combined with a naso-frontal hinge — missing in the tinamou and the ratites. Just why these schizorhinal bills take advantage of both methods of hinging is still not solved. But it would appear that the normal elevation of the whole bill may take place under the action of *M. protractor quadrati* and that the elevation of just the bill tip may occur when the bill is driven into the mud. The contraction of *M. depressor mandibulae* under such conditions would apply pressure to retract the quadrate as mentioned for the woodcock. So the same action that lowers the lower bill slightly, against the resistance of the hole, would also elevate the very tip or "nail" of the bill. At any rate, as illustrated in Fig. 13, there is a gradual bending of the bill in its long mid-portion where premaxilla and the paired maxillae are weak, with a notable movement of the tip and a notable movement at the naso-frontal hinge.

The Gaping Adaptation. — For greater completeness, brief mention is made of a skull adaptation involving reduction of the adductor musculature with increase in protractor musculature. This adaptation, which calls for the use of the bill as a pry, is more widespread in birds than may be suspected. I have previously mentioned (Beecher, 1950, 1951) the importance of this adaptation in the American blackbirds family Icteridae, and (Beecher, 1953) made scattered reference to it throughout the songbirds. A fairly detailed treatment of its significance in the starlings, family Sturnidae, is in preparation.

Very briefly, the adaptation involves an enormous forward spread of the origin of *M. protractor quadrati* on the interorbital septum for powerful elevation of the upper bill tip and even greater spread of the origin of *M. depressor mandibulae* for the forceful lowering of the mandible. The latter muscle spreads its origin over the whole posterior area of the skull, and its insertion on an extension of the retroarticular process (Fig. 2) of the mandible posterior to its cranial articulation, gives it great leverage. Birds equipped with this adaptation use the bill as a pry, for probing in the ground, lifting leaf litter in search of insects, etc. As in shorebirds, the contraction of *M. depressor mandibulae* (Fig. 2, 1) creates a pressure on the quadrate which rocks it backward on the cranial articulation to aid powerfully the elevation of the upper bill tip by the contraction of *M. protractor quadrati* (2).

The Wood-pecking Adaptation. — Only brief mention will be made, also, of the wood-pecking adaptation. I have pointed out previously (Beecher, 1953b) the enormous evolutionary development of *M. protractor quadrati* in woodpeckers (family Picidae), and true nuthatches (family Sittidae). This muscle serves a powerful antagonistic function against the entire pterygoideus musculature to form a muscular shock absorber, relieving some of the shock to the braincase in the rapid and repeated chisel-action of these species. The palate is, thus, held in resilient rigidity by the action of these antagonists, one of which would elevate the upper bill, the other, depress it. The interorbital septum is a fairly thick wall of bone with the fenestrae greatly reduced, and there is a massing of bone in the region of the nano-frontal hinge.

DISCUSSION

We have seen some of the adaptations, evolved by special groups of birds, within the general adaptational framework of the kinetic skull. There are many other variations that would be worthy of attention. Even the small adaptational differences between related species with slightly differing diet would be rewarding subjects for the research of a graduate student ; and a thorough study of all members in any avian family would be full of surprises. The writer hopes to survey the non-passerine families in future papers, but only in broad outlines.

It must be obvious that a specialization such as the kinetic bird skull did not spring up full-blown in Aves. Kinetic skulls occur in fishes, early amphibians, and reptiles — particularly snakes. Versluys (1910) points out that kinesis was characteristic of many dinosaurs, most of which had a metakinetic skull like present-day *Sphenodon*, the New Zealand tuatara. This was a skull in which the rostral portion could rotate on the pivot of the basipterygoid process to elevate and depress the large snout relative to the insignificant cranium. The hinge in such metakinetic skulls was far posterior, caudal to the parietals. Such skulls lack the streptostylic or free quadrate required for the bird skull.

But, as Versluys points out, some of the dinosaurs had mesokinetic skulls like birds. *Creosaurus* had its hinge between frontals and parietals, and the streptostylic quadrate was hinged to the cranium. Versluys believed *Archaeopteryx* — the strange bird-dinosaur of the Jurassic — to have been mesokinetic. But I must agree with Simonetta (1960) that there seems to be no good evidence of this. In fact, it seems necessary to place this species off to the side of the main path of avian evolution, both on this count and because of the complete lack of a keel. More than one line of bird-footed dinosaur may have crossed the threshold and become birds. To be the ancestor of all living and fossil birds (except *Archaeopteryx*), the ancestral bird must have had at least the beginnings of a mesokinetic skull.

Except to disagree on this one point, I have no intention of going into a subject so well-covered by Versluys and others.

Once the forelimbs began to be modified into wings, the strange, feathered creature — running along branches and leaping out in semi-gliding flight to escape enemies — was committed. As wings evolved, the kinetic bill had to evolve. Perhaps the "proof" is that the ratites — birds which lost flight to re-occupy the ground niche of the extinct dinosaurs — have reduced kinetics. Simonetta is quite certain that the elephant birds, Aepyornithidae, had completely akinetic skulls. If so, we have come full circle in our study. But *did* they have? We do not know the musculature of these extinct birds, but the quadrate looks functional in his drawings. I am reminded of the kiwi, and find it hard to believe in muscles that do not move anything or specialized bones that do not function.

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